

# An early Late Cretaceous mammal from Japan, with reconsideration of the evolution of tribosphenic molars

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**Abstract.** The morphology of a mandibular fragment with a left lower molar discovered in the “Upper Formation” (upper Cenomanian lower Turonian) of the Mifune Group in central Kyushu, southwestern Japan, suggests that this fossil should be assigned to a new species of Late Cretaceous mammal, *Sorlestes mifunensis* sp. nov. (Infraclass Eutheria ; Order Proteutheria ; Family Zhelestidae). *S. mifunensis* is the oldest zhelestid yet recorded. Some workers suggest that the Zhelestidae have a close affinity with ungulates. A detailed comparison between the lower molar of the new species and those of ungulates supports this suggestion. The comparison also suggests that the Zhelestidae have a closer affinity with ungulates than the Zalambdalestidae and other contemporary mammals, and that *S. mifunensis* has a relatively primitive character within the Zhelestidae. This comparison leads us to revise the diagnoses of the family Zhelestidae and of the genus *Sorlestes*. The unique character of the entoconid-hypoconulid twinning seen in the Zhelestidae was probably caused by the movement of the hypoconid (the presumed first single talonid cusp seen in the first therian *Kuehneotherium*) to the buccal side, far away from the other talonid cusps. This twinning pattern is distinct from the twinning pattern seen in marsupials.

**Key words :** Japan, Late Cretaceous, Mesozoic mammal, Mifune Group, *Sorlestes*, tribosphenic molar

## Introduction

It is generally believed that tribosphenic mammals first appeared around the Jurassic-Cretaceous boundary (Bown and Kraus, 1979 ; Kielan-Jaworowska et al., 1979b ; Sigogneau-Russell, 1991). They are ancestors of the eutherian and metatherian mammals which probably differentiated during the Neocomian (Early Cretaceous) (Kielan-Jaworowska et al., 1979a ; Cifelli, 1993 ; Eaton, 1993 ; Wang et al., 1995). The eutherian orders radiated widely at the beginning of the Tertiary. However, recent fossil finds suggest that the eutherian orders may have originated and differentiated in the Late Cretaceous (Fox and Youzwyshyn, 1994 ; Archibald, 1996 ; Gheerbrant et al., 1996).

Until 20 years ago there were only very few reports of tribosphenic mammals from the early Late Cretaceous (Cenomanian-Santonian). This situation has, however,

changed and many such fossils are now known from this period (Cifelli and Eaton, 1987 ; Cifelli, 1993 ; Eaton, 1993 ; Nesson et al., 1994 ; Nesson et al., 1998). In particular, Nesson et al. (1994) report many early Late Cretaceous tribosphenic mammals from Middle Asia (Uzbekistan, Kazakhstan and Tajikistan).

In the present study, we document a mammal fossil specimen, which was first reported by Setoguchi (1992), from the “Upper Formation” (upper Cenomanian-lower Turonian ; lower Upper Cretaceous) of the Mifune Group in central Kyushu, southwestern Japan. The specimen is a small mandibular fragment with a tribosphenic lower molar. The new find is significant because it is the only known example of a mammal fossil from the Late Cretaceous eastern coastal lowlands of the Asian Continent. The other Asian Late Cretaceous mammal fossils, in contrast, come from either inland deposits or deposits along the Tethys sea and the

Turgai Strait of that time (Clemens *et al.*, 1979; Nessov *et al.*, 1994).

The tooth nomenclature used in this contribution is that of Bown and Kraus (1979) and Nessov *et al.* (1998).

### Geological setting

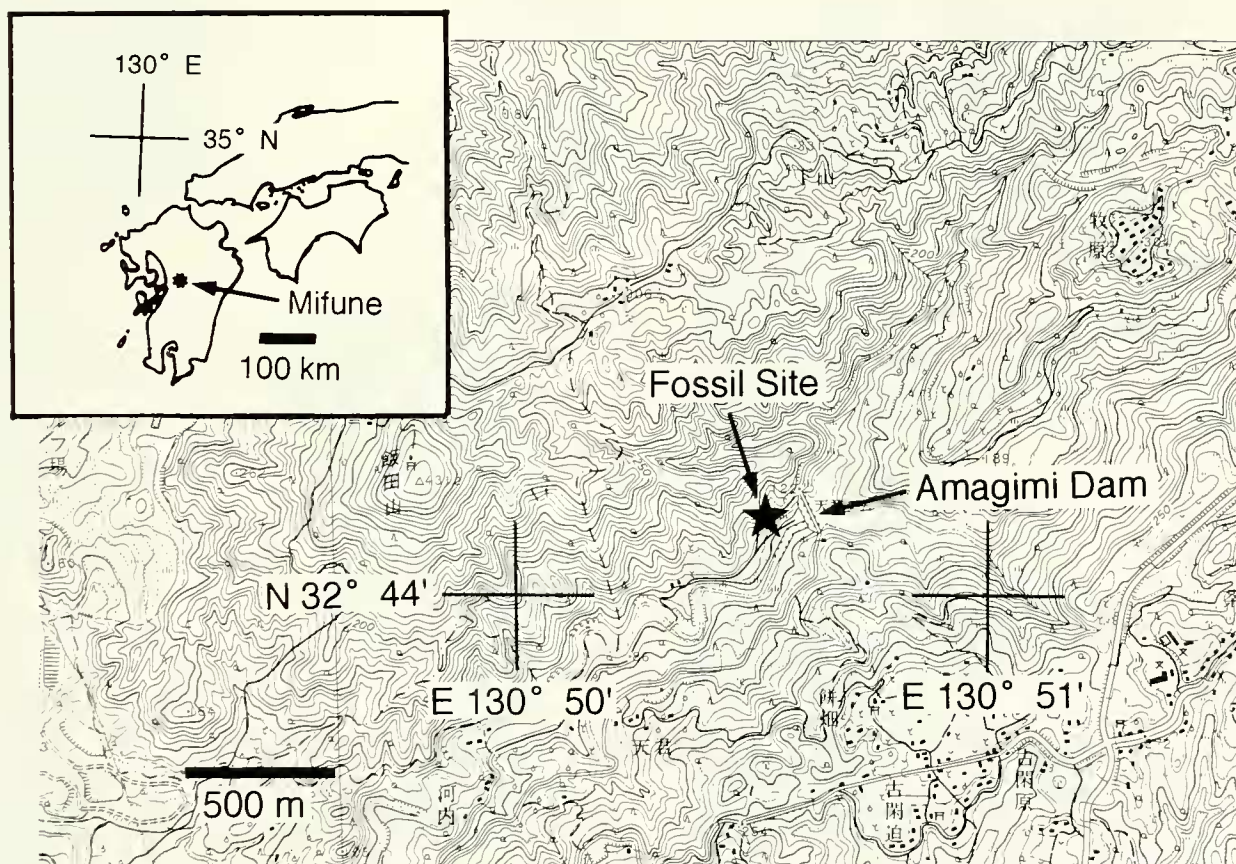
The present fossil material was discovered in the "Upper Formation" of the Mifune Group, which is distributed in the Mifune Town area of Kumamoto Prefecture, central Kyushu, southwestern Japan (Figure 1). The Mifune Group unconformably overlies green schist associated with serpentinite in the northern area, and the Upper Permian Mizukoshi Formation in the southern area (Matsumoto, 1939). The Mifune Group is, in turn, unconformably overlain by the Upper Cretaceous Gankaizan Formation (Tamura and Tashiro, 1966). The Mifune Group is considered to be early Late Cretaceous in age (see below), and to have formed in a sedimentary basin situated on the east coastal margin of the Late Cretaceous Asian Continent.

The Mifune Group has a total thickness of about 1,500 m and consists of "Basal", "Lower" and "Upper" formations (Matsumoto, 1939). The lowermost or "Basal Formation" is

dominated by conglomerate and very coarse-grained sandstone (Matsumoto, 1939), yielding fresh-water bivalves, such as *Trigonioides*, (Tamura, 1979; Matsumoto *et al.*, 1982). The middle or "Lower Formation" is dominated by sandstone and sandy mudstone (Matsumoto, 1939), yielding brackish-water and shallow-marine molluscan fossils, such as *Inoceramus concentricus costatus* and *Eucalycoceras* sp. cf. *E. spathi* of middle Cenomanian age (Tamura and Matsumura, 1974; Tamura, 1979; Matsumoto *et al.*, 1982). The uppermost or "Upper Formation" is dominated by red mudstone (Matsumoto, 1939), yielding non-marine bivalves (Tamura, 1979) and several vertebrate fossils, such as dinosaurs, pterosaur, and the present specimen (Tamura *et al.*, 1991; Setoguchi, 1992; Okazaki and Kitamura, 1996).

The Gankaizan Formation, which unconformably overlies the Mifune Group, consists of conglomerate, coarse-grained sandstone and red mudstone (Tamura and Tashiro, 1966; Matsumoto *et al.*, 1982), yielding *Inoceramus* (*Platyceramus*) *amakusensis*, of lower Santonian age, in its upper part (Tamura and Tashiro, 1966; Matsumoto *et al.*, 1982).

The present fossil material comes from the upper part of the "Upper Formation" near the Amagimi Dam, Mifune Town (Figure 1). The stratum where the fossil was discovered



**Figure 1.** Topographic map showing the fossil locality, near the Amagimi Dam, Mifune Town, Kumamoto Prefecture, Kyushu, southwestern Japan (a part of topographic map "Mifune", 1 : 25,000 scale, Geographical Survey Institute of Japan).



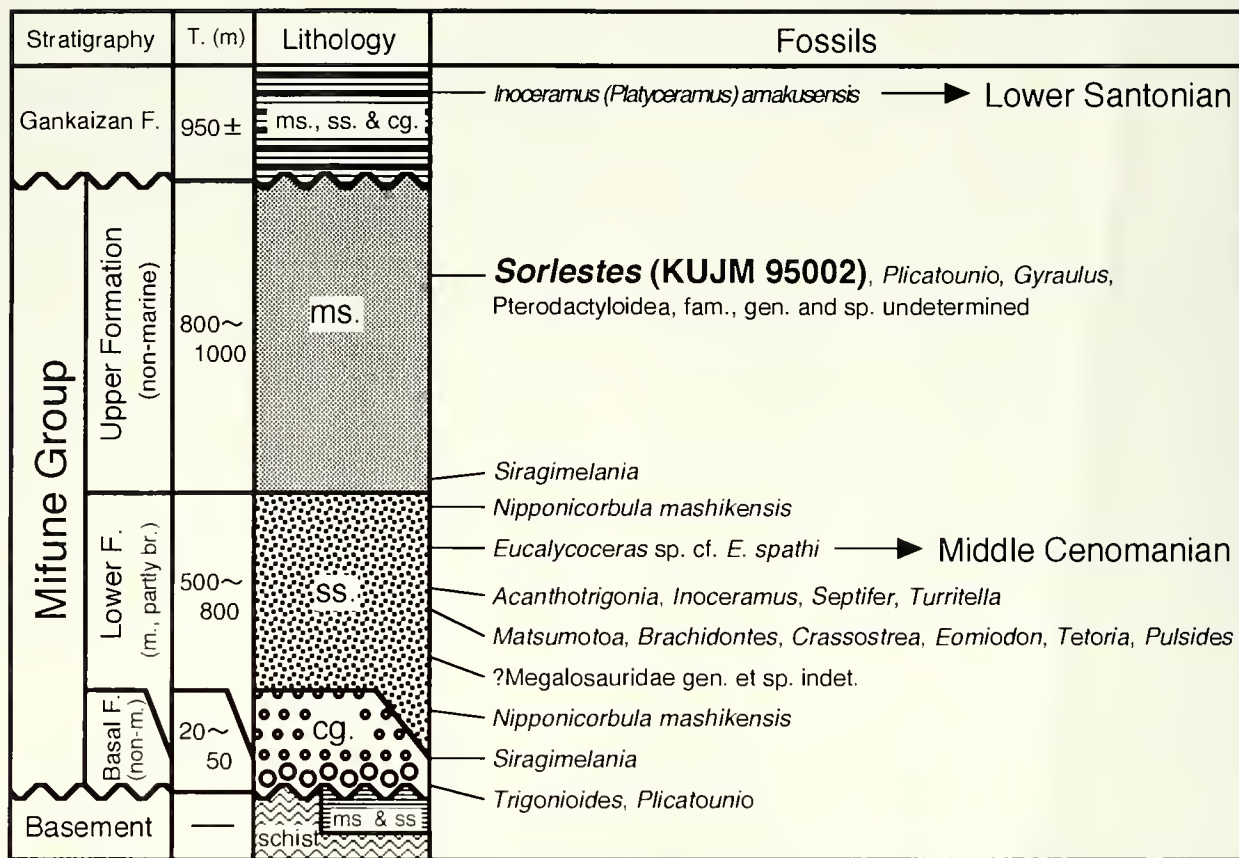


Figure 2. Stratigraphy of the Cretaceous deposits in the south of Kumamoto City, Kyushu, Japan (modified from Matsumoto, 1939; Tamura and Tashiro, 1966; Matsumoto et al., 1982; Tamura et al., 1991; Hasegawa et al., 1992; Okazaki and Kitamura, 1996). Abbreviations: m., marine; br., brackish; T., thickness; ms., mudstone; ss., sandstone; cg., conglomerate.

consists of coarse-grained sandstone. The age of the "Upper Formation" is considered to be late Cenomanian to early Turonian on the basis of the ages of the Lower Formation and the Gankaizan Formation. A synthetic scheme of the stratigraphy of the Mifune Group is shown in Figure 2.

### Systematic paleontology

Class Mammalia Linnaeus, 1758  
 Infraclass Eutheria Gill, 1872  
 Order Proteutheria (Romer, 1966) Butler, 1972  
 Family Zhelestidae (Nessov, 1985) Nessov, 1990

**Revised diagnosis.**—The upper and lower molars are typical tribosphenic types. The protocone is large and mesiodistally expanded. The styler shelf is relatively narrow, but the parastylar region is wide and expanded mesially bearing two cusps. A small paraconid is displaced relatively lingually and relatively close to the metaconid. Compared with other proteutherians, the trigonid height is lower relative to talonid height. The talonid is about as wide as the trigonid and mesiodistally longer and lower than the trigonid.

The talonid basin is deep and open lingually, so that the deepest part of the talonid basin is situated at its lingual margin. The entoconid and hypoconulid are markedly close to one another, and are quite clearly separated from the hypoconid.

The upper and lower last premolars are premolariform (*sensu* Krishtalka, 1976), but the upper one has a incipient metacone. In occlusal view, the upper one is somewhat mesiodistally constricted between the paracone and the protocone.

Genus ***Sorlestes*** Nessov, 1985

**Type species.**—*Sorlestes budan* Nessov, 1985.

**Included species.**—*S. budan* Nessov, 1985; *S. kara* Nessov, 1993; *S. mifunensis* sp. nov.

**Revised diagnosis.**—The paraconid is not strongly appressed to the metaconid. The protoconid is larger than in *Aspanlestes* (Zhelestidae). The entoconid is very markedly close to the hypoconulid (entoconid-hypoconulid twinning), and both are located at the distolingual corner of the talonid, opposite the hypoconid which is located at the distobuccal corner. The cristid obliqua extends just below the notch of

the protocristid between the protoconid and the metaconid.

***Sorlestes mifunensis* sp. nov.**

Figure 3

*Holotype*.—KUJM 95002, a left mandibular fragment with a molar. (KUJM means Kyoto University, Japan, Mesozoic)

*Hypodigm*.—The type specimen only.

*Etymology*.—Named after Mifune Town, where the type specimen was discovered.

*Repository*.—Department of Geology and Mineralogy, Division of Earth and Planetary Sciences, Graduate School of

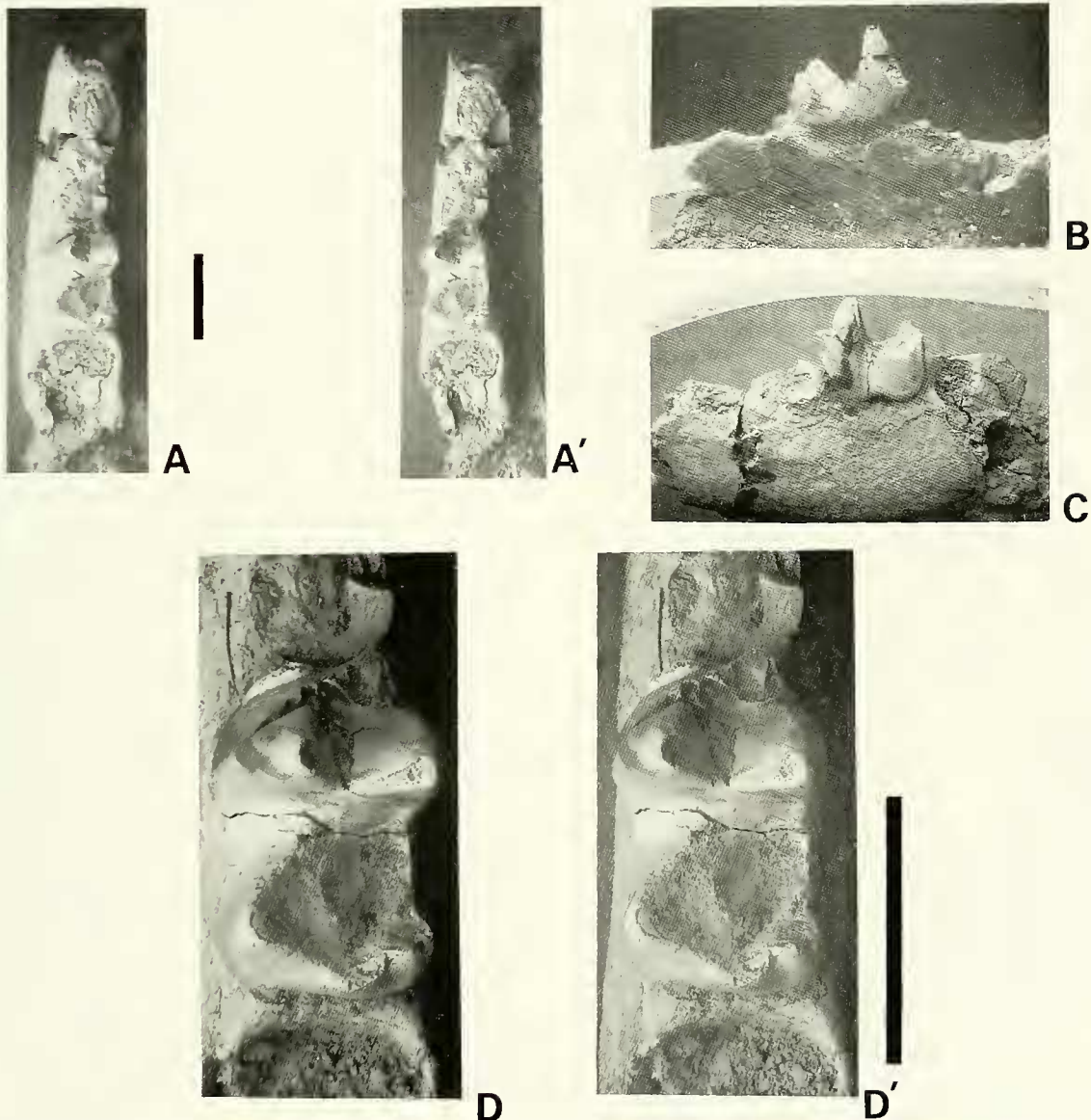
Science, Kyoto University, Japan.

*Locality*.—Lat. 32°44'09" N; Long. 130°50'32" E: Loc. 1 of Tamura *et al.* (1991, fig. 1; Figure 1), near the Amagimi Dam, Mifune Town, Kumamoto Prefecture, Kyushu, southwestern Japan.

*Horizon*.—Upper part of the "Upper Formation", Mifune Group (Figure 2).

*Age*.—Late Cenomanian to early Turonian; Late Cretaceous.

*Diagnosis*.—The lower molar of *S. mifunensis* is almost as large as *S. budan*, and larger than *S. kara*. Compared to *S. budan*, the paraconid is less appressed to the metaconid, and the entoconid and hypoconulid are closer together.



**Figure 3.** *Sorlestes mifunensis* sp. nov., KUJM 95002, holotype. **A, A'**, occlusal view (stereophotographic pair). **B**, lingual view. **C**, buccal view. **D, D'**, occlusal view of the preserved molar (stereophotographic pair). Scale bars=2 mm (left scale corresponds to A, A', B, C, right scale corresponds to D, D').



**Description.**—The type specimen (KUJM 95002) is a fragmentary left mandible with a molar. The preserved part of the mandibular ramus is about 8 mm in length, and about 4 mm in height and about 2 mm in width below the preserved molar. Immediately mesial to the molar, there is a broken root, which is circular and not compressed anteroposteriorly in occlusal view (Figures 3-A, A'). Immediately distal to the molar, there is a broken alveolus. Mental foramen could not be identified in KUJM 95002.

The protoconid of the preserved molar is much larger and higher than the metaconid, and leans somewhat lingually. The metaconid is situated just lingual to the protoconid. Although badly broken at the base, it is clear that the paraconid is near the anteroposterior midline, and less anteriorly appressed than in *S. budan*. There is no crest joining the paraconid with the metaconid. A distinct precingulid runs downward from the mesiobuccal base of the paracristid notch, disappearing at the buccal base of the protoconid. The posterior trigonid wall is almost vertical, and nearly perpendicular to the mandibular extension.

The talonid is longer than wide. It is longer than, as wide as, and roughly half as tall as the trigonid. The hypoconid and entoconid are almost the same height, and somewhat higher than the hypoconulid. The hypoconulid is only very slightly projected posteriorly. The entoconid and hypoconulid are closer together than in *S. budan*, and are located at the distolingual corner of the talonid. A very weak postcingulid runs down buccally from the hypoconulid, disappearing at the buccal base of the hypoconid. The deepest part of the

talonid basin is situated at its lingual margin, so that the deep talonid basin is open lingually, and inclined lingually as a whole. The cristid obliqua originates directly below the notch between the protoconid and the metaconid, and is much higher than the entocristid. The hypoflexid is well-formed and deep.

Wear facets can be observed from the tip of the protoconid to the tip of the metaconid through the protoconid. The tips of the hypoconid, hypoconulid and entoconid are slightly worn. The talonid basin is also worn (although the effects of secondary erosion are difficult to assess), which forms a U-shaped "wear facet".

Dental measurements are given in Table 1 and Figure 4.

## Discussion

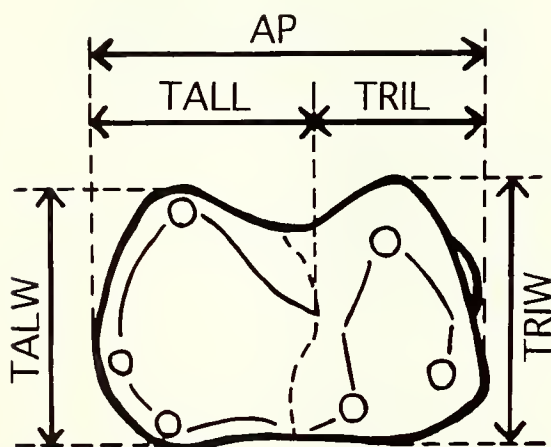
### Identification of the present lower molar

The tooth class of the molar preserved in KUJM 95002 can be identified as  $M_2$ , because the trigonid is as wide as the talonid which is the same as on  $M_2$  of *S. budan*. The possibility that it should be identified as  $M_1$  cannot, however, be immediately excluded. As Lillegraven (1976) pointed out, it is a usual therian condition that the paraconid is most buccally set on  $M_1$  and becomes progressively more lingual on  $M_2$ – $M_3$ . Furthermore, Cretaceous eutherians characteristically have a protoconid that leans somewhat more lingually on  $M_1$  than that on  $M_2$ , so the distance between the tip of the protoconid and that of the metaconid in occlusal view is shorter on  $M_1$  than that on  $M_2$ . These characters are also observed in the zhelestid *Asparlestes* (Nessov *et al.*, 1994, pl. 4, fig. 1). KUJM 95002 shows a combination of these  $M_1$  characters.

In either case, KUJM 95002 and *S. budan* clearly have distinct lower molar structures (see diagnosis of *S. mifunensis*). *S. kara*, another species of *Sorlestes*, has much smaller molar size than KUJM 95002. We, therefore, consider KUJM 95002 to be a new species of *Sorlestes*.

### Phyletic position of *Sorlestes mifunensis*

Phylogenetic relationships of the Zhelestidae have been discussed by various workers (Figure 5). Lillegraven (1976) described *Gallolestes*, which was subsequently classified as belonging to the Zhelestidae by Nessov *et al.* (1994), based on the lower molar morphology. Lillegraven (1976) favors eutherian affinities for *Gallolestes*, and points out the similarities between *Gallolestes* and hyopsodontid condylarths. Butler (1977), however, points out that *Gallolestes* shares some derived characters of the lower molars with *Zalambdalestes* (Proteutheria; Zalambdalestidae) and with *Purgatorius* (Primate), and he doesn't exclude the possi-



**Figure 4.** Orientations of the measurements of lower molars (modified from Nessov *et al.*, 1994). Buccal to top of page; anterior to right. Abbreviations are shown in Table 1.

**Table 1.** Measurements (in mm) of the preserved molars of the type specimens of *Sorlestes mifunensis* sp. nov. The measurements are oriented as shown in Nessov *et al.* (1994, fig. 1; see Figure 4). Abbreviations: AP, anteroposterior length; TRIL, trigonid length; TALL, talonid length; TRIW, trigonid width; TALW, talonid width.

	[mm]	AP	TRIL	TALL	TRIW	TALW
KUJM 95002 ( <i>S. mifunensis</i> ) left lower molar ( $M_1$ or $M_2$ )		2.60	1.15	1.45	1.75	1.70

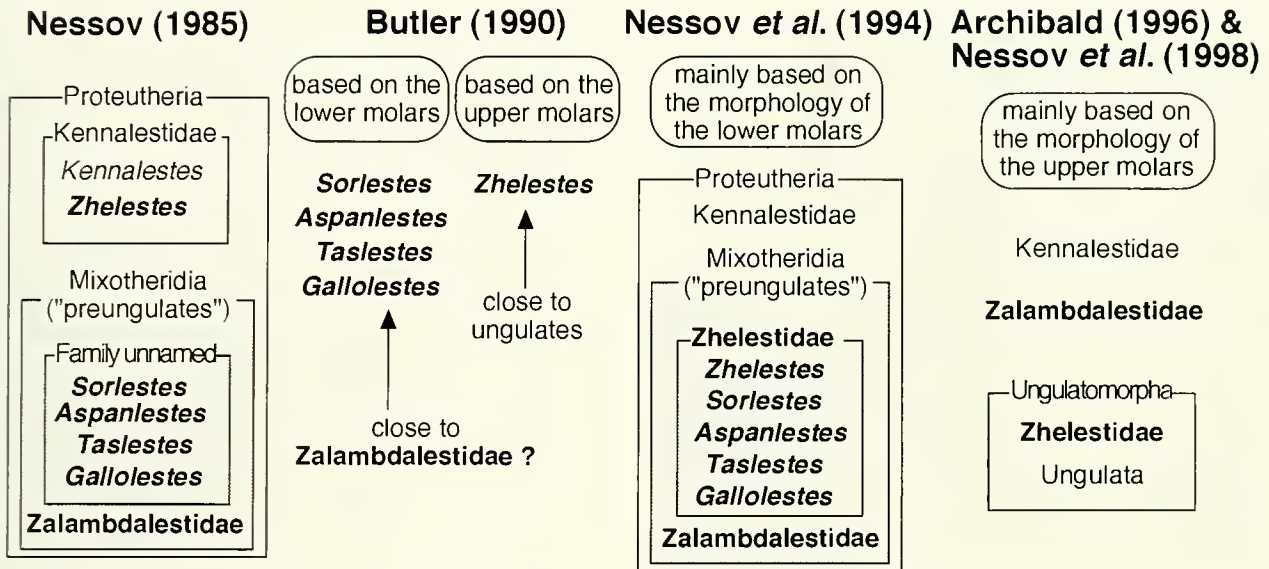


Figure 5. The classifications and phylogenetic relationships used in recent studies for the Zhelestidae.

bility of a relationship between *Gallolestes* and *Protungulatum* (Condylarthra). Clemens (1980) concludes that *Gallolestes* is possibly a representative of another lineage of metatherian-eutherian grade of dental evolution that cannot be assigned to either the Eutheria and Metatheria.

Based on the lower molar morphology, Nesson (1985) suggests that *Taslestes*, *Aspanlestes*, *Sorlestes* and *Gallolestes* should be combined in the same taxonomic group, a group which was subsequently classified as belonging to the Zhelestidae in Nesson et al. (1994). Nesson (1985) proposed a new suborder Mixotheridia (Proteutheria) including both the above genera and the Zalambdalestidae, and suggested that this suborder was related to condylarths. In the same paper, he described a new genus *Zhelestes*, based on the upper dentition. He classified it into the new subfamily Zhelestinae (Proteutheria; Kennalestidae), and at this time didn't include it in the Mixotheridia. Later, he raised this subfamily to the family level (Nesson, 1990). Butler (1990) points out that the zalambdalestids differ from *Aspanlestes*, *Sorlestes* and *Gallolestes* in some molar features, suggesting that relationships of these genera to zalambdalestids is not impossible, but it needs to be substantiated. He also considers that *Zhelestes* might be an earlier representative of condylarths. According to Nesson et al. (1994), the Zhelestidae include *Gallolestes*, *Taslestes*, *Aspanlestes* and *Sorlestes*, and these are all included in the suborder Mixotheridia along with the Zalambdalestidae. They consider the Mixotheridia (both the Zhelestidae and the Zalambdalestidae) to be "preungulates". In contrast, based mainly on the upper molar's morphology, Archibald (1996) and Nesson et al. (1998) consider that the Zhelestidae are sister groups of ungulates, and the Zalambdalestidae are only distantly related to them.

In this paper, we follow the suggestions of Archibald (1996) and Nesson et al. (1998). The reasons for our preference are briefly summarized below.

On the basis of the lower molar structure, Nesson et al. (1994) claimed that both the Zhelestidae and the Zalambdalestidae are closely related to ungulates. However, the two families show the following differences: (1) The Zhelestidae have more low-crowned lower molars with a trigonid that is less elevated to the talonid (Butler, 1990). (2) The paraconid and metaconid in the Zhelestidae are less closely appressed than in the Zalambdalestidae. (3) The Zhelestidae have a lingually open talonid, whereas the talonid is lingually closed in the Zalambdalestidae (see Kielan-Jaworowska, 1984, pl. 14, 15). In these features, the Zhelestidae are morphologically more similar to early ungulates than to the Zalambdalestidae. Most early ungulates (for instance, *Protungulatum*, *Diacodexis*, and so on) share the diagnostic characteristics of zhelestids, that is, the high, large, wide and lingually open talonid with the hypoconulid situated markedly close to the entoconid, and the rather lingually displaced paraconid with some appression to the metaconid (see McKenna, 1960, figs. 52, 53, 56, 57; Archibald, 1982, figs. 56, 60; Estravis and Russell, 1989, pl. 1; Rose, 1996, fig. 1). This combination of characteristics is not seen in any other contemporary mammal. For example, in *Purgatorius*, an early primatomorphan, the talonid is large, wide and high, but is closed lingually with the hypoconulid situated centrally (see Clemens, 1974, fig. 2; Buckley, 1997, fig. 1). In *Gypsonictops*, a Late Cretaceous insectivore, the talonid is large, wide and somewhat lingually open. However, the hypoconulid is centrally situated, and the paraconid is situated rather centrally than lingually (see Clemens, 1973, figs. 1, 4; Cifelli, 1990, fig. 2).

Based mainly on an analysis of upper molar morphology, Archibald (1996) and Nesson et al. (1998) suggest that the Zalambdalestidae does not have a close affinity with ungulates. Similarly, a study of lower molar morphology indicates that the Zhelestidae most closely resemble early ungulates. The lingually closed talonid in the Zalambda-



lestidae, which is shared by many other eutherians, may be an apomorphic character which zhelestids and early ungulates do not possess (see below). This would imply that the Zalambdalestidae should be excluded from a very close relationship with ungulates. In support of this idea, some workers (Van Valen, 1964; McKenna, 1975; Stucky and McKenna, 1993; Archibald, 1996) consider the Zalambdalestidae to be more closely related to *Anagale* and rabbits.

Compared with the Zhelestidae, early ungulates have a relatively high talonid with robust cusps on the lower molars. Compared to the other representatives of the Zhelestidae, *Sorlestes mifunensis* shows a primitive characteristic in that the paraconid is less appressed to the metaconid.

Nesov (1993) created a new family Kulbeckiidae (consisting of a single new genus *Kulbeckia*) within the Mixotheriidae. In the Kulbeckiidae, the hypoconulid is markedly close to the entoconid, and the paraconid is lingually situated with appression to the metaconid, similar to the Zhelestidae. Unfortunately, it is not clear whether the talonid is open or not in the Kulbeckiidae, so it is difficult to discuss any possible relationship between the Zhelestidae, Kulbeckiidae and other mammals.

### Evolution of tribosphenic molars

The most characteristic feature of *Sorlestes mifunensis* is the lower molar with the hypoconulid situated markedly close to the entoconid, quite clearly opposed to the hypoconid. This twinning pattern is rarely seen in other Cretaceous eutherians, in which the hypoconulid is centrally located between the hypoconid and the entoconid. The recognition of this character prompted us to reconsider the evolution of the talonid cusps. It seems that the talonid cusps developed along with the occluding upper tooth and the adjacent lower tooth.

**1. First cusp formed in the talonid of *Kuehneotherium*, the first therian mammal:** The earliest therian mammal, *Kuehneotherium*, had already appeared by the Norian (Late Triassic) (Fraser *et al.*, 1985). In the lower molars of *Kuehneotherium*, the tallest and largest cusp can be recognized as homologous with the protoconid of the later tribosphenic molars. The other two cusps, which are situated mesiolingually and distolingually from the protoconid, can likewise be identified as equivalents of the paraconid and metaconid, respectively (Kermack *et al.*, 1968). These homologies of the trigonid cusps are now not really in debate (Slaughter, 1971).

In the lower molars of *Kuehneotherium*, there is, however, a unicuspid distal heel or talonid, posterior to the trigonid (Kermack *et al.*, 1968, fig. 3). The homology of this cusp has been discussed by several workers (Slaughter, 1971; Clemens and Lillegraven, 1986), and the two main opinions are that it corresponds to either the hypoconid or hypoconulid.

Mills (1967) used the occlusal relationship between the upper and lower molars to propose that the single talonid cusp of Jurassic pantotheres corresponds to the hypoconid on the basis of the occlusal relationship between the upper and lower molars. The same conclusion was also reached by Freeman (1979) and Prothero (1981). In contrast, Kermack

(1967) interpreted the single talonid cusp in Welsh pantotheres (*Kuehneotherium*) as the hypoconulid on the basis of the relationship between the talonid and its following tooth. Crompton (1971), Slaughter (1971) and Butler (1978) also correlated this cusp with the hypoconulid, although the latter didn't completely exclude the possibility that it could represent the hypoconid.

The next stage in evolution toward the tribosphenic molar is seen in *Amphitherium* or *Palaeoxonodon*, whose talonid extends distobuccally from the base of the metaconid and bears a large single cusp at its distobuccal margin (Simpson, 1928, fig. 38; Freeman, 1979, pls. 16, 17). In *Palaeoxonodon*, there is a small cusplule at the approximate median point of the oblique crest which links the metaconid and a large single talonid cusp (Freeman, 1979). Further development is seen in *Peramus*. In this genus the talonid bears two or three cusps, identified as the hypoconid, hypoconulid and entoconid of the tribosphenic molar (Clemens and Mills, 1971; Clemens and Lillegraven, 1986). The talonid basin is not fully basined and is open lingually (Clemens and Mills, 1971, pl. 3).

By comparing the molar morphology of the animal mentioned above with later tribosphenic mammals, we consider that the single talonid cusp seen in *Kuehneotherium* corresponds to the hypoconid, as proposed by Mills (1967). This suggestion is also supported by the following arguments. (1) We would like to stress the occlusal relationship between the upper main cusp (paracone) and the first talonid cusp. The paracone is the largest cusp in the upper molar and is functionally very important for masticating foods. We, therefore, propose that the occlusal relationship between the paracone and the single talonid cusp, as well as between the paracone and the protoconid, is likely to be maintained in the therians. (2) In *Amphitherium* or *Palaeoxonodon*, the talonid extends distobuccally from the base of the metaconid and bears a large single cusp at its distobuccal margin, where the hypoconid of the tribosphenic molar is situated. (3) We propose, furthermore, that the groove separating the hypoconid and the hypoconulid in tribosphenic molars is also significant. This groove is deeper and stronger than the groove separating the hypoconulid and the entoconid, so the hypoconulid and entoconid are likely to be related more closely to each other than to the hypoconid. (4) Freeman (1979) stated that in certain specimens of *Palaeoxonodon* there is an incipient development of the entoconid and hypoconulid in addition to the large talonid cusp situated distobuccally.

We, therefore, propose the following sequential development. The first talonid cusp seen in *Kuehneotherium* corresponds to the hypoconid, and the entoconid and hypoconulid appeared at some later stage, being more closely related to each other than to the hypoconid.

**2. Entoconid hypoconulid twinning:** The primitive talonid for a tribosphenic molar envisaged by most workers is basined and lingually opened with a relatively large hypoconid, smaller hypoconulid and in some cases also an entoconid (Clemens and Lillegraven, 1986; Szalay, 1994). Examination of Early Cretaceous tribosphenic mammals suggests that the roughly centrally placed hypoconulid

between the hypoconid and the entoconid may also be a primitive characteristic.

In Late Cretaceous mammals, the lower molars of many eutherians have a centrally-placed hypoconulid. In contrast, the molars of contemporary marsupials have a hypoconulid twinned with an entoconid. In this respect the molars of the eutherian Zhelestidae resemble those of marsupials. However, the twinning in the Zhelestidae is clearly distinct from that in marsupials (Figure 6).

In marsupials, the hypoconulid is distolingually displaced compared to the Zhelestidae. The twinning pattern seen in the Zhelestidae is associated with a primitive-type talonid as seen in the tribosphenic pattern. This association suggests that the twinning seen in the Zhelestidae is more primitive than in marsupials. The twinning pattern seen in the Zhelestidae is likely to have been caused by the movement of the hypoconid to the buccal side far away from the other talonid cusps, corresponding to the expansion of the protocone of the upper molars (Archibald, 1996; Nessov *et al.*, 1998). The twinning pattern seen in marsupials is more likely to be a secondary feature (Cifelli, 1993), and could be functionally related to the early trend of the enlargement of the metacone and reduction of the paracone in this group (Clemens and Lillegraven, 1986).

The entoconid-hypoconulid twinning is also related to the position of the paraconid of the posterior molar. This is because the paraconid fits into the groove between the hypoconulid and the entoconid of the anterior tooth. In many eutherians, the paraconid is situated centrally,

because the hypoconulid of the anterior tooth is centrally-placed between the hypoconid and the entoconid, and the groove between the hypoconulid and the entoconid is situated more buccally. In the Zhelestidae, the paraconid is situated more lingually than centrally, because the hypoconulid is situated lingually and twinned with the entoconid, and the groove between the two cusps is situated more lingually than centrally. In marsupials, the paraconid is situated more mesiolingually than in eutherians (include the Zhelestidae), because the hypoconulid of the anterior tooth is situated more distolingually and twinned with the entoconid, and the groove between the two cusps is situated far more distolingually.

As mentioned above, the lingually open talonid with a hypoconulid markedly close to the entoconid as seen in the Zhelestidae is probably a reflection of the primitive state. This condition is also seen in early eutherian like *Prokennalestes* (Kielan-Jaworowska and Dashzeveg, 1989, figs. 26, 27), but not seen in early metatherian, *Kokopellia* (Cifelli, 1993, fig. 1).

#### Co-evolution of mammals and plants

The age from the Albian to the Cenomanian was a very important period for the mammalian evolution. At this time the flora underwent a change from one dominated by ferns and gymnosperms to one with abundant angiosperms. Flowering angiosperms appeared at the beginning of the Cretaceous, and very rapidly became a major plant group (Crane, 1987; Collinson, 1990). Angiosperms have leaves,

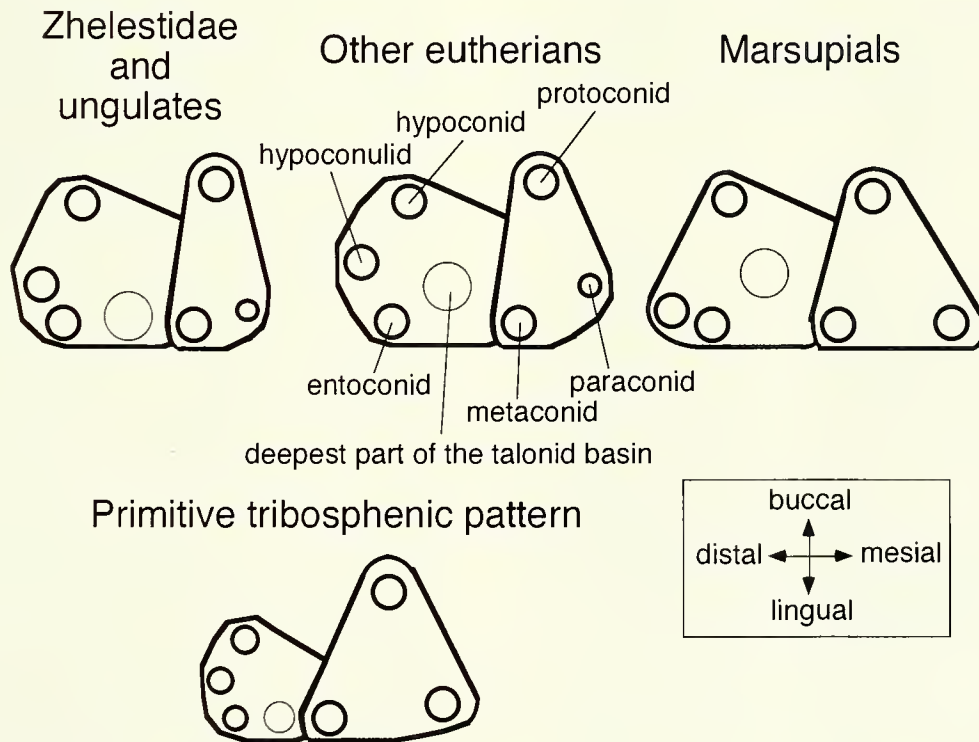


Figure 6. Comparisons of the lower molar patterns of tribosphenic mammals (occlusal view of the left lower molars).



flowers, fruit, pollen and honey. In other words, these plants have foods with high nutritive value. It was for this reason that insects began to evolve explosively at this time. It follows, therefore, that insectivorous mammals, whose staple foods were insects and/or larvae of insects, also began to increase in numbers and diversity. The mammals who began to diversify and radiate in this way are the Cretaceous tribosphenic mammals. The period when the Mifune Group was deposited is the very period when angiosperms had become a major plant group, and when insectivorous mammals like *Sorlestes* evolved rapidly.

### Conclusions

Morphological studies of the mammalian remain discovered from the lower Upper Cretaceous Mifune Group in central Kyushu, southwestern Japan suggest that it should be assigned to a new species of the genus *Sorlestes* (Order Proteutheria; Family Zhelestidae), and is here named *S. mifunensis*.

The lower molars of the Zhelestidae exhibit a series of ungulate-like characteristics. It suggests that the Zhelestidae and early ungulates are far more closely related to each other than to the Zalambdalestidae and other mammals. The twinning pattern of the hypoconulid and entoconid in the Zhelestidae, including *Sorlestes mifunensis*, shows a more primitive state than that of metatherians and most of the other eutherians.

*Sorlestes mifunensis* is the oldest known zhelestid yet recorded, and suggests that the origin of ungulates perhaps goes back even further to the early Late Cretaceous, or at least, that mammals having ungulate-like characters had already been differentiated by the late Cenomanian to early Turonian. The find of *Sorlestes mifunensis* also indicates that zhelestid existed not only in western Asia but also on the coastal plain of eastern Asia.

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